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# Effects of four mono- and sesquiterpenes on the consumption of alfalfa pellets by sheep[1,2]

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**ABSTRACT:** Effects of individual terpenes on alfalfa pellet intake by lambs were examined in four experiments. Forty-five lambs (nine lambs/treatment) were individually fed alfalfa pellets sprayed with either camphene, myrcene, caryophyllene oxide, or $\beta$-pinene at one of five concentrations (one terpene per experiment). Treatments (0, 0.5, 1, 2, and 10×) were multiples of the concentration (×) of a specific terpene in tarbush. Terpenes were applied to alfalfa pellets (0.64 kg·lamb$^{-1}$·d$^{-1}$, DM basis), and consumption was measured during a 20-min interval for 5 d. Lambs were maintained and fed alfalfa pellets in one group (except during 20-min tests) at a mean total daily intake of 4.7% of BW (DM basis). Camphene and caryophyllene oxide tended to decrease intake (linear contrasts were $P$ = .0651 and $P$ = .0504, respectively), whereas myrcene and $\beta$-pinene exerted no effect on the consumption of alfalfa pellets by lambs. Camphene and caryophyllene oxide may be involved in the differential herbivory of individual tarbush plants by livestock.

Key Words: Food Intake, Food Preferences, Herbivores, Sheep, Terpenoids

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## Introduction

Shrubs have become a dominant component of the Chihuahuan Desert landscape during the past 100 yr (Fredrickson et al., 1998). These shrubs are often avoided by livestock even though they are highly nutritious. Terpenoids and phenolics are typically antiherbivory compounds in desert shrubs (Meyer and Karasov, 1991). One native shrub that has increased on the Jornada Experimental Range at the expense of desert grasslands on the heavier, more productive soils is tarbush (*Flourensia cernua* DC; Buffington and Herbel, 1965). This shrub is high in crude protein (16 to 25%, depending on phenology) and contains substantial quantities of terpenes and phenolics (Estell et al., 1996b). Livestock will consume tarbush in limited amounts under free-ranging conditions (Nelson et al., 1970; Anderson and Holechek, 1983), depending on the season and availability of other forages, but this shrub is not a preferred species. Sheep can eat tarbush in mixed diets for several weeks without exhibiting symptoms of toxicosis or abnormal digesta kinetics or fermentation patterns (Fredrickson et al., 1994; King et al., 1996). Ruminants exhibit differential selectivity among plants when forced to consume this shrub (Estell et al., 1994b). Differential use was related to the quantity of epicuticular wax on the leaf surface of tarbush (Estell et al., 1994b), and removal of compounds with organic solvents increased preference by sheep for this shrub (Estell et al., 1994a). Specific mono- and sesquiterpenes on the leaf surface of tarbush were related to tarbush use based on multivariate analyses (Estell et al., 1998a); however, specific compounds must be tested individually to prove cause and effect (Clausen et al., 1992). Several volatile compounds previously shown to be related to tarbush intake (camphor, borneol, limonene, *cis*-jasmone, $\alpha$-pinene, $\beta$-caryophyllene, *p*-cymene, $\alpha$-humulene, 1,8-cineole, 3-carene, and sabinene) have been examined (Estell et al., 1998b, 2000), but only two monoterpenes (camphor and $\alpha$-pinene) were related to intake by lambs when tested individually.

The objective of the following experiments was to individually examine effects of four additional terpenes on the intake of alfalfa pellets by lambs. Our hypothesis was that consumption of alfalfa pellets by lambs would decrease as the concentration of a specific terpene increased.

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[2]Mention of a trade name, proprietary product or vendor does not constitute a warranty of the product by the USDA or imply its approval to the exclusion of other products or vendors that may also be suitable.

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## Materials and Methods

### *Treatments, Animal Management, and Experimental Protocol*

Four experiments were conducted to examine individual effects of three hydrocarbon monoterpenes (camphene, myrcene, and $\beta$-pinene) and an oxygenated sesquiterpene (caryophyllene oxide) on intake of alfalfa pellets by sheep. Caryophyllene oxide was related to tarbush in one of our previous studies (Estell et al., 1996a) and camphene, myrcene, and $\beta$-pinene were related to herbivory in other studies using ruminants (Personius et al., 1987; Riddle et al., 1996). Mean concentrations of each chemical on the surface of tarbush leaves in previous studies (Estell et al., 1994b, 1996a; Tellez et al., 1997; approximately 100, 100, 30, and 20 μg/g DM for camphene, myrcene, caryophyllene oxide, and $\beta$-pinene, respectively) were considered as the concentration (×) to which livestock would be exposed when browsing tarbush. One terpene was examined at five concentrations (treatments) in each experiment. Treatments were multiples (0, 0.5, 1, 2, or 10) of the exposure concentration (×) for that specific compound. Treatments were relative to a positive control within each study (ethanol without terpene) and a negative control (consumption of all 45 lambs without ethanol) in wk 2.

Experiments were conducted in accordance with USDA guidelines, and protocols were approved by the New Mexico State University Institutional Animal Care and Use Committee. The experimental protocol followed Estell et al. (2000). Forty-five ewe lambs (Polypay, approximately 5 mo of age, mean initial BW of 36.8 ± 0.42 kg, without previous browsing experience) were randomly assigned to 1 of 15 pens and three groups (pen and group assignment were constant across experiments). Before each experiment, lambs were randomly assigned to one of the five terpene concentrations (nine lambs per treatment, restricted to three lambs per treatment in each group) using a randomized complete block design.

Lambs were individually fed treated pellets each morning during a 20-min interval. The three groups (15 individually penned lambs per group) were fed in succession at 0800, 0830, and 0900 in an enclosed metabolism unit (1.22- × 2.44-m pens). Each experiment was 5 d in length, with two preliminary 5-d periods to familiarize lambs with handling procedures and 20-min feeding (wk 1) and to establish baseline intake of alfalfa pellets during the 20-min interval without treatments (wk 2). Camphene, myrcene, caryophyllene oxide, and $\beta$-pinene treatments were examined during wk 3 through 6, respectively, with the order of testing selected randomly, and with a 2-d interval between experiments. During the 20-min feeding, 0.64 kg of alfalfa pellets (DM basis; ≥ 15% CP; 0.95 cm diameter; from sun-cured alfalfa hay) were offered daily to each lamb. Orts were recorded daily and lambs were weighed on d 5 each week before the 0800 feeding. Alfalfa pellets were sampled randomly throughout the study, composited, ground to pass a 2-mm screen in a Wiley Mill, and analyzed for dry matter (94.9%; AOAC, 1990).

Lambs were adapted to alfalfa pellets for 2 wk and the drylot pen for 1 wk before individual feeding began. Lambs were maintained together in a drylot with free access to water and trace-mineralized salt (93 to 97% NaCl, 3 g/kg Mn, 2.5 g/kg Zn, 1.5 g/kg Fe, 0.15 g/kg Cu, 0.09 g/kg I, 0.025 g/kg Co, and 0.01 g/kg Se), except during 20-min feeding periods, and were group-fed untreated pellets twice daily in addition to the treated pellets (mean total daily intake = 4.7% of BW, DM basis). Lambs were fed at 1000 (adjusted weekly for growth; mean ADG = 0.24 ± 0.005 kg/d) and 1300 (0.95 kg DM·lamb$^{-1}$·d$^{-1}$). An amount of untreated alfalfa pellets equal to the orts during the 20-min tests was also fed at 1000. During the 2-d intervals between experiments, lambs were group-fed an additional 0.64 kg DM·lamb$^{-1}$·d$^{-1}$ of untreated feed at 1000.

All compounds were purchased from Aldrich Chemical (Milwaukee, WI) except myrcene, which was purchased from Sigma (St. Louis, MO). Manufacturer specified purities were 95, 90, 99, and 99% for camphene, myrcene, caryophyllene oxide, and $\beta$-pinene, respectively. Stock solutions of these four chemicals containing 20, 20, 6, and 4 mg/mL in 100% ethanol, respectively, were diluted 5-, 10-, and 20-fold in ethanol. Application of stock and 5-, 10-, and 20-fold dilutions at 0.05 mL/g of DM corresponded to 10×, 2×, 1×, and 0.5× treatments, respectively. The control (0×) alfalfa pellets were sprayed only with ethanol. Treatment solutions were stored in amber glass containers and applied with graduated (34-mL increments) polyethylene spray bottles in a stream pattern to minimize volatilization. Pellets were added to one end of the stainless steel feed pans and repeatedly tilted during treatment application. Order of application was rotated systematically within and across days, and an approximately 10-min interval occurred between spraying and feeding. An exhaust fan was operated in the metabolism unit, and treatments were applied in an adjacent room with separate ventilation. Lambs were maintained outdoors until immediately before the 20-min feeding.

Chemical loss due to volatilization between application and feeding was examined for each compound using modifications of Estell et al. (2000). Stock solution (17 mL) was sprayed on 0.32 kg of alfalfa pellets (DM basis) in quadruplicate for each chemical. At 2, 10, 20, and 30 min after spraying, the entire sample was transferred to a flask, and 350 mL of 100% ethanol was added (including pan rinse). Samples were sealed and extracted for 6 h with constant shaking, filtered through a glass fiber filter, diluted to approximately 15 ng/μL, and analyzed with gas chromatography/mass spectrometry (**GC/MS**; six injections per sample), using instrumentation parameters and column conditions as described by Tellez et al. (1997) and external standard

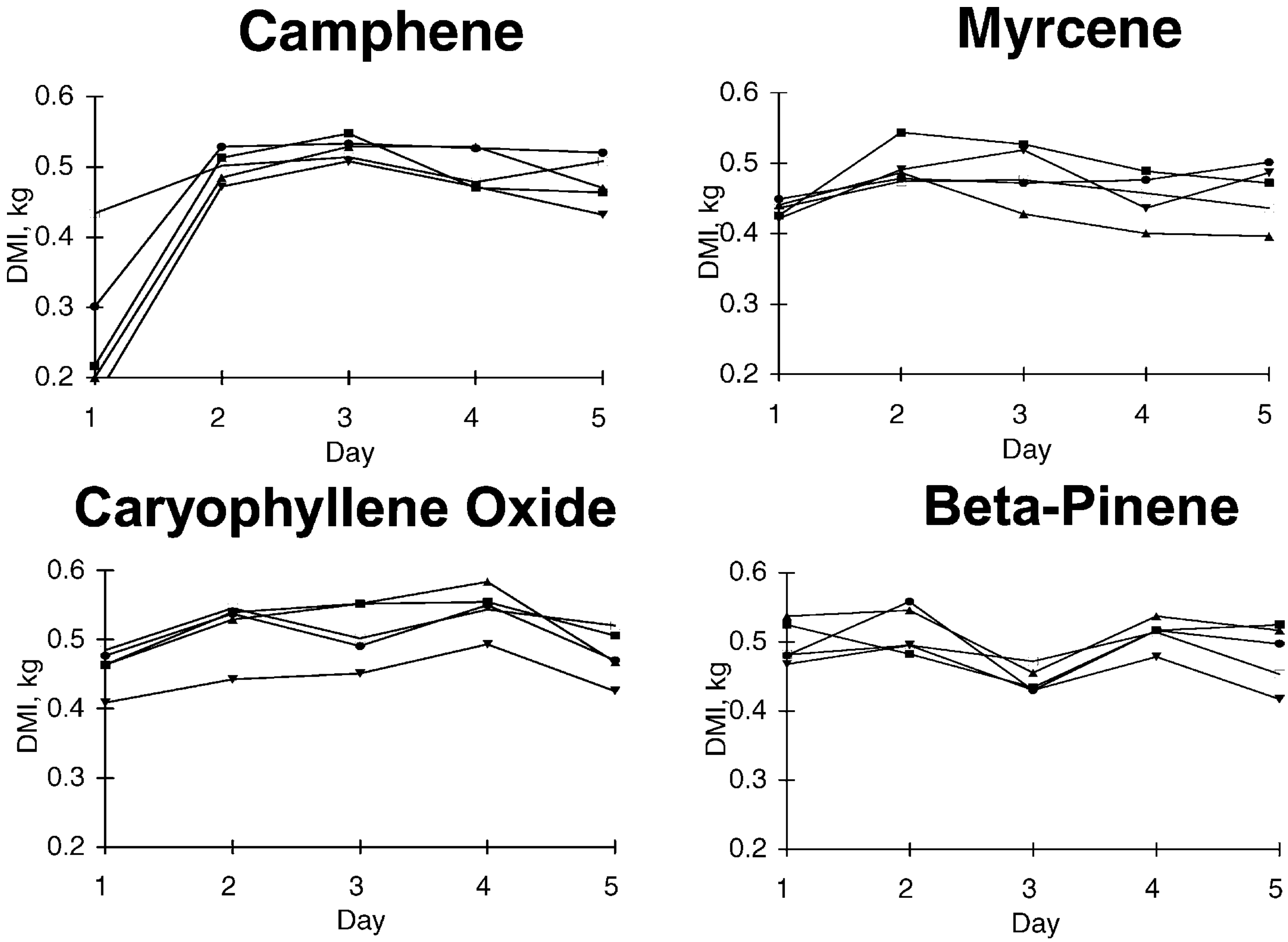


**Figure 1.** Mean intake of treated alfalfa pellets by lambs (n = 9 lambs/treatment) during a 20-min interval. Treatments (multiples of the concentration of specific compounds in tarbush) are designated ❐, ●, ■, ▲, and ▼ for 0×, 0.5×, 1×, 2×, and 10×, respectively.

curves for quantitation. Extraction efficiency was determined for each compound by adding 17 mL of each stock solution to 0.32 kg of pellets in a sealed flask. After standing for 30 min, 350 ml of ethanol was added, flasks were resealed and extracted for 6 h with continual shaking, extracts were filtered, diluted to approximately 15 ng/μL, subjected to GC/MS analysis (six injections per sample), and quantified with external standard curves. Recovery at each time post-spraying was corrected for extraction efficiency. Extractions of alfalfa pellets without treatments (ethanol only) were conducted as described above to determine background concentrations of compounds in alfalfa pellets. The corrected mean recovery at 2, 10, 20, and 30 min, respectively, was 83.8, 62.5, 55.4, and 40.4% for camphene; 88.2, 79.7, 65.5, and 58.5% for myrcene; 100.0, 98.9, 97.2, and 97.7% for caryophyllene oxide; and 92.3, 92.8, 81.0, and 77.2% for $\beta$-pinene. The 10-min sampling time equates to the beginning of the 20-min feeding period (an approximate 10-min lag between spraying and feeding). None of four terpenes examined were present above the detection limits of GC/MS in untreated alfalfa pellets. Caryophyllene oxide (a sesquiterpene) was almost completely nonvolatile and exhibited little difference between 2 and 30 min. As expected, the three monoterpenes (particularly camphene) were more volatile than caryophyllene oxide.

### *Statistical Analysis*

An analysis of variance was conducted for each experiment using GLM procedures of SAS (SAS Inst., Inc., Cary, NC) with pellet consumption (5-d means) during the 20-min interval as the dependent variable and treatment (terpene concentration) and group (block) as the independent variables in the model. Pen and animal are confounded and pen was not in the model; however, no pen effects were observed under similar conditions in a previous study (Estell et al., 1998b). Orthogonal contrasts were constructed for unequally spaced treatment levels to identify linear and quadratic effects of treatment on intake in each experiment. Also, intake

**Table 1.** Mean consumption by lambs during a 20-min interval of alfalfa pellets treated with terpenes[abc]

| Concentration | Adaptation | Camphene | Myrcene | Caryophyllene oxide | $\beta$-Pinene |
|---|---|---|---|---|---|
| | kg·lamb$^{-1}$·d$^{-1}$, DM basis | | | | |
| 0×[d] | 0.52 | 0.49 | 0.46 | 0.52 | 0.48 |
| 0.5× | | 0.48 | 0.48 | 0.51 | 0.50 |
| 1× | | 0.44 | 0.49 | 0.52 | 0.50 |
| 2× | | 0.44 | 0.43 | 0.52 | 0.52 |
| 10× | | 0.41 | 0.47 | 0.44 | 0.46 |
| SEM | | 0.030 | 0.034 | 0.033 | 0.029 |

[a]Concentrations of compounds applied to alfalfa pellets were multiples (0, 0.5, 1, 2, or 10) of the concentration of that compound in tarbush (×); n = 9 lambs/treatment.
[b]No ethanol was applied during the adaptation period.
[c]Linear treatment responses for camphene and caryophyllene oxide were $P$ = 0.0651 and $P$ = 0.0504, respectively. Linear and quadratic day × treatment interactions were detected ($P$ < 0.05) for camphene.
[d]Means within a row for the control treatment (0×) did not differ ($P$ = 0.1599); n = 45 for wk 2 and n = 9 in wk 3 to 6; SEM = 0.012 in wk 2 and 0.028 for wk 3 to 6.

of control lambs (n = 45, SEM = 12.4 for wk 2, n = 9, SEM = 27.8 for wk 3 to 6) was subjected to analysis of variance with week as the independent variable to evaluate the consistency of intake of control lambs over time. Means were separated ($P$ < 0.05) by LSD (SAS Inst., Inc.) in the case of a significant $F$-value ($P$ < 0.05). Repeated measures analysis of variance was conducted for each experiment using GLM procedures of SAS with day, treatment, and group as independent variables to ensure that day × treatment interactions did not preclude analysis of data pooled across days. Orthogonal polynomial contrasts were tested among days in this analysis.

## Results and Discussion

Repeated measures analyses indicated a linear and quadratic treatment effect for wk 3 ($P$ < 0.05). Low intakes for lambs on all treatments except the control on d 1 in this experiment (Figure 1) likely account for the significant day × treatment interaction for camphene. Intake of control lambs during wk 2 was not different from that of controls in other weeks ($P$ > 0.05; Table 1). Control lambs received pellets treated with the ethanol in wk 3 to 6, but not during wk 1 or 2; however, treatment of alfalfa pellets with ethanol did not affect intake by lambs previously (our unpublished observations). Because lambs were fed at a constant percentage of body weight, intake of controls was not expected to vary among weeks.

Both camphene and caryophyllene oxide tended to exhibit a linear intake response to treatment concentration (Table 1; linear contrasts for wk 3 and 5 were $P$ = 0.0651 and $P$ = 0.0504, respectively). The reduction in intake of lambs on the 10× treatments relative to controls was approximately 16 and 14% for camphene and caryophyllene oxide, respectively. Effects of chemicals are not directly comparable because of the confounding effects of time and because treatment levels varied based on their concentration in tarbush leaves. Also, volatility (based on recovery values) of caryophyllene oxide was lower than for the three monoterpenes; thus, the actual level of exposure was less affected by time after application.

Individual terpenes have been shown to be related to plant use for a number of mammalian species. Bucyanayandi et al. (1990) examined the bark of four conifer species and found that for the two species without meadow vole damage, two monoterpenes (including myrcene) were present only in undamaged seedling species. Zhang and States (1991) observed a negative relationship between the concentration of three monoterpenes (including myrcene) and feeding by Abert squirrels on ponderosa pine trees. Snyder (1992) reported two monoterpenes (including $\beta$-pinene) were lower in the resin of ponderosa pine trees selected by Abert squirrels, and both were deterrent in subsequent feeding studies. Epple et al. (1996) found pocket gophers consumed less food from feeding stations and avoided areas scented with a commercial pine needle oil ($\beta$-pinene and myrcene among its constituents).

Little information is available concerning the involvement of specific terpenes in ruminant diets. Personius et al. (1987) reported that specific monoterpenes were related to differential use within and among various sagebrush taxa by mule deer, including camphene, which was greater in the most preferred species. Several monoterpenes were positively (including camphene) or negatively (including myrcene and sabinene + $\beta$-pinene) correlated to intake of juniper by goats (Riddle et al., 1996). Previously at this location, when a mixture of cattle, sheep, and goats were forced to use tarbush, they exhibited differential use of tarbush plants, and caryophyllene oxide was in the subset of important variables for distinguishing between high-, moderate-, and low-use plants when subjected to multivariate analysis (Estell et al., 1996a).

Our results were partially consistent with our previous observations and with effects reported in the literature for other mammalian species. Myrcene and $\beta$-pinene did not deter feeding by sheep, in contrast to previous findings for small mammals. Camphene was positively related to intake in previous reports, in contrast to our results. We are not aware of other studies that examined the relationship of caryophyllene oxide and diet selection. However, this sesquiterpene exhibited a very low volatility (based on its high recovery) and had a clear effect on intake for the 10× treatment (Figure 1).

Volatile substances are particularly effective herbivory defense mechanisms because herbivores are repelled before any damage to the plant occurs (Levin, 1976). Many terpenoids are compartmentalized in glandular trichomes; consequently, these compounds are concentrated at the site of exposure to herbivore sense organs (Personius et al., 1987). Radwan and Ellis (1975) reported a greater total emission of volatile monoterpenes from Douglas fir clones that were resistant to browsing than from genotypes susceptible to deer browsing. Mayland et al. (1997) demonstrated that volatiles (primarily green leaf volatiles) released from different cultivars of tall fescue were related to preference or intake by cattle.

Discrepancies between this study and previous research may be due in part to the fact that most studies reporting relationships of volatiles with herbivory were correlative in nature, rather than singular application of specific compounds. Moreover, compounds such as myrcene could be part of a synergystic or cumulative effect, because total terpene concentration has been related to intake by ruminants in other studies (Schwartz et al., 1980; Yabann et al., 1985). Recent work in Australia suggests that volatile compounds may serve as cues for the detection of other compounds. 1,8-Cineole was reported to be negatively related to intake by various marsupials consuming eucalyptus, but it was subsequently shown to simply be correlated with concentration of other aversive compounds and to serve as a cue to detect these toxins (e.g., jensenone; Lawler et al., 1998, 1999). Also, many of the studies that suggest terpenes are related to dietary preferences used animals on a low plane of nutrition, whereas the lambs in our study were fed a high-quality diet at nearly 5% of BW. Nutrient status may affect preference, and animals on a higher plane of nutrition may consume more aversive phytochemicals (Illius and Jessop, 1996; Wang and Provenza, 1996), which might explain a lack of effects by two terpenes in our study. In contrast, Burritt et al. (2000) did not observe increased intake by lambs of a mixed diet containing sagebrush with either energy or protein supplementation; however, Banner et al. (2000) reported that energy supplementation did increase sagebrush intake by lambs when components were fed separately.

The quantities of compounds needed to conduct research in large mammals can be prohibitive in some situations. Also, in many of the studies described above, animals had opportunity to select among various plants, whereas lambs in the present study had no opportunity to exhibit preference. Initial eating rate during a short interval at the beginning of the feeding period is a good criterion with which to measure palatability, and doing so minimizes the confounding of palatability and postingestive effects (Baumont, 1996). However, no evidence of postingestive aversion to terpenes was observed in our studies. The only significant day effect identified by repeated measures analysis was due to increased intake of all camphene treatments except the control between d 1 and 2 (Figure 1). Although monoterpenes are typically toxic to insects, they are generally safe for consumption by mammals (Rice and Coats, 1994). In fact, many monoterpenes are listed as “Generally Recognized as Safe” for use in food flavorings, cosmetic fragrances, and pharmaceuticals used by humans (Rice and Coats, 1994) and therefore make logical candidates for manipulation of selectivity by grazing mammalian herbivores.

In summary, two of the compounds examined had no effect on intake, and two other compounds depressed intake; thus, results partially support our hypothesis. However, effects were minimal except with the 10× treatment (Table 1). Nevertheless, camphene and caryophyllene oxide are two leaf surface compounds that may explain part of the differential use of tarbush by ruminants. Other factors yet to be determined (e.g., other terpenes, other classes of chemicals, and synergystic/cumulative effects) are likely involved in this phenomenon as well.

## Implications

Two of the four terpenes examined in this study affected the consumption of alfalfa pellets by lambs when fed individually for a short time without the potential for synergism among terpenes or a choice of alternative feed. Understanding the role of specific plant chemicals in the mediation of plant–animal interactions is crucial to the development of mechanisms for altering the behavior and selectivity of livestock that will lead to an increased use of presently avoided shrubs as a nutrient source. However, the benefits of increased shrub consumption would depend on the balance of nutritional benefits and metabolic impacts of phytotoxins.

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